Organismal and Evolutionary Biology Research Programme
Faculty of Biological and Environmental Sciences
Doctoral Programme in Plant Sciences (DPPS)
University of Helsinki
Helsinki

EFFECTS OF MICROCLIMATIC VARIATION OF SNOWMELT AND TEMPERATURE ON SUBARCTIC-ALPINE AND ARCTIC PLANTS

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DOCTORAL DISSERTATION

To be presented for public examination with the permission of the
Faculty of Biological and Environmental Sciences of the
University of Helsinki, in lecture theatre B3, Forest Sciences building,
Latokartanonkaari 7, Helsinki University Viikki Campus,
on the 17th of May, at 12 o'clock.

Helsinki 2019

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ISBN 978-951-51-5239-8 (paperback)
ISBN 978-951-51-5240-4 (Online, http://ethesis.helsinki.fi)
ISSN 2342-5423 (paperback)
ISSN 2342-5431 (Online, http://ethesis.helsinki.fi)

Unigrafia, Helsinki 2019

Svalbard

Here, the spirits rule the seasons
With their magic and their might
Bringing summer, spring and autumn
And the endless winter night

You may think that it is cruel
Bitter cold and biting gusts
So to find this place's beauty
Is a little of a quest

Only when a solar storm
Hits the earth's magnetosphere
And the darkness of the night
Is exquisitely clear
Light unfolds across the sky
In the colours of your dreams
The Aurora Borealis
Is much more than what it seems
Spirits cast this spectacle
Across the winter canopy
To remind us how unearthly
Nature's beauty may well be

Ice and snow seem endless here
Brutal, restless, breath-taking
But their power is not evil
As their duty's life-guarding
Underneath the shielding snow
Life survives the winter's cold
To the spirits, perseverance,
Is a virtue to behold
When the winter with its hardship
Has been born for long enough
From the thawing springtime sparseness
Life revives from barren soil

One may find a revelation
In the talent of such force
How extraordinary beauty
Such adversity can forge

ABSTRACT

Climate change will be most pronounced at high latitudes where it will affect autumn, winter and spring disproportionally more than the growing season. Increasing or decreasing precipitation as snow, rising temperature and more frequent freeze-thaw cycles raise uncertainties about how the timing of snowmelt and the length of the growing season will change for northern plants. The timing of plant developmental stages (phenophases) in relation to snowmelt timing is important for avoiding harsh weather conditions in spring and ensuring a long growing season.

In this doctoral dissertation, I investigate the effect of snowmelt timing and temperature conditions on plant phenology and plant stress.

The first objective was to determine the natural variation in snowmelt timing on a small spatial scale in subarctic-alpine Finland. Such variation in the microclimate is created by the landscape topography and show the range of conditions plant populations are currently adapted to. Snowmelt timing varied by up to seven weeks within a few metres distance, so that early-melting plots were exposed to more frequent and more severe spring freezing events. This implies that plant populations are already exposed to the kind of climatic conditions which would be predicted from climate change.

Secondly, I studied how the physiology of *Vaccinium vitis-idaea* and the phenology of seven subarctic-alpine plant species are affected by this natural variation in microclimate. The higher numbers of freezing events in early-melting plots were related to a higher reduction in the quantum yield of photosystem II (Φ_{PSII}) in *V. vitis-idaea*, but not to increases in frost damage. This species therefore does not suffer substantial damage from the natural climatic variation in this habitat, implying that in this location it is likely highly resistant to the predicted changes in climate. Differences in snowmelt timing also led to three distinct patterns of phenological timing in subarctic-alpine plant species along the snowmelt gradient. These patterns can raise ideas about the mechanisms underlying the rate of plant development and can help researchers classify past and future phenological responses.

Lastly, I compare the effect of natural versus experimental gradients of snowmelt timing on the timing of autumn senescence in High Arctic plants. The results show that the two gradients lead to different conclusions regarding the effect of snowmelt timing on the timing of

autumn senescence. Selective warming only in the beginning of autumn had a delaying effect on autumn senescence in *Dryas octopetala*, despite the short duration of the warming treatment. Previous studies have commonly employed a warming treatment over the entire growing season.

The results of this dissertation highlight that we need to integrate different approaches to studying climate change effects on plants. Natural gradients, although often disregarded, can give additional insight into plants' adaptation to climate variation and therefore complement experiments. Experimental treatments simulating climate change need to be very selective in which period of the plant life cycle they are applied as expected changes in climate strongly depend on the season. Due to the variable sensitivity of different phenophases and plant species to climate and the importance of plants in the ecosystem carbon balance, further detailed research is needed to understand the drivers and mechanisms underlying plant phenology.

CONTENTS

LIST OF ARTICLES

This thesis is based on the following articles:

I Gehrmann, F., Hänninen, H., Liu, C. and Saarinen, T. (2017). Phenological responses to small-scale spatial variation in snowmelt timing reveal compensatory and conservative strategies in subarctic-alpine plants. *Plant Ecology & Diversity* 10:453-468.

II Gehrmann, F., Lehtimäki, I.-M., Hänninen, H. and Saarinen, T. Subarctic-alpine *Vaccinium vitis-idaea* exhibits resistance to strong variation in snowmelt timing and frost exposure, suggesting high resilience under climatic change. (*manuscript*)

III Gehrmann, F., Ziegler, C. and Cooper, E.J. Natural and experimental snowmelt gradients lead to divergent conclusions about climate change effects on autumn senescence in High Arctic plants. (*manuscript*)

The articles are referred to in the text by their roman numerals.

Table of Contributions

	I	II	III
Original idea	FG, TS	FG, TS	FG, EC
Study design	FG, TS	FG, TS	FG, EC, CZ
Data collection	FG, CL	FG, IML, CL	FG, CZ
Analyses	FG	FG, IML	FG
Manuscript preparation	FG, CL, TS, HH	FG, IML, TS, HH	FG, EC, TS, HH

FG: Friederike Gehrmann, TS: Timo Saarinen, HH: Heikki Hänninen, IML: Iida-Maria Lehtimäki, EC: Elisabeth Cooper, CZ: Camille Ziegler.

ABBREVIATIONS

ATP	adenosine triphosphate
CO2	carbon dioxide
DAS	days after snowmelt
DOY	day of year
F_v/F_m	ratio of variable to maximum fluorescence of photosystem II
F_v	variable fluorescence of photosystem II
F_m	maximum fluorescence of photosystem II
PAR	photosynthetically active radiation
UV	ultraviolet
Φ_{PSII}	Quantum yield of photosystem II

1 INTRODUCTION

1.1 SNOW IN SUBARCTIC-ALPINE AND ARCTIC ECOSYSTEMS

The tundra biome at high northern latitudes consists of the Arctic, which is botanically defined as the area north of the edge where trees are capable of growing (treeline), and the subarctic-alpine region, which are the mountaneous areas above the altitudinal treeline situated between the closed-canopy boreal forest to the south and the Arctic treeline to the north (Murray et al. 1998; Huntington 2001). In these treeless ecosystems, winter is characterised by long-lasting snow cover which has a strong influence on plant life (Jonas et al. 2008; Estilow et al. 2015). Snow has a low thermal conductivity, which insulates the plants beneath the snow cover from low and fluctuating air temperatures in winter and spring, which could cause severe frost damage on plants. Beneath the snow, the heat transfer from the soil keeps the temperature near the ground close to 0 °C, even when the regional air temperature is considerably lower, providing a stable thermal environment for roots and microorganisms and affecting the depth of soil frost (Pomeroy and Brun 2001). A relatively thin snowpack of about 20-30 cm is sufficient for preventing the freezing of soil water, which could lead to the desiccation of plant tissue as transpired water cannot be replaced adequately (Larcher 1957; Sakai 1968; Tranquillini 1982; Groffman et al. 1999). The slow diffusion through snow cover also increases the moisture and the concentration of carbon dioxide beneath the snow, especially if ice lenses are present in the snow pack (Fahnestock et al. 1998, Musselman et al. 2005). Furthermore, depending on the thickness and the structure of the snowpack, photosynthetically active radiation (PAR) can be transmitted through the snow (Gerland et al. 2000). Consequently, conditions under the snow can be favourable for photosynthesis in early and late winter, with the exception of the period of polar night at high latitudes.

During spring, the melting snow pack locally provides a slow and steady release of water and nutrients to the adjacent plants which can continue long into the summer for late-melting snowbeds (Björk and Molau 2007; Clement et al. 2012). The thinning of the snowpack allows increasing amounts of light to reach the underlying plants and coincides with a lengthening of the photoperiod (at moderately high latitudes) and

increasing temperatures, so that the timing of snowmelt is the main determinant of the onset of plant growth. Therefore, despite being generally only present in the winter, snow strongly affects the life of plants during their subsequent most active period in spring and summer.

1.2 CLIMATE CHANGE EFFECTS ON SNOW AND TEMPERATURE CONDITIONS FOR SUBARCTIC-ALPINE AND ARCTIC PLANTS

Climate change is predicted to affect especially winter conditions and cause more extreme changes in high northern latitudes than elsewhere. For northern Finland, a reduction in the amount of snowfall by up to 60 % and a shortening of the snow covered period by up to 30 % have been predicted to occur by 2100 compared to the reference period (1961-1990; Jylhä et al. 2009). Overall, temperature is predicted to rise twice as fast in the Arctic compared to the global mean with a disproportionally stronger warming in autumn compared to summer (Chylek et al. 2009; Serreze et al. 2009; IPCC 2013). Furthermore, increases in the frequencies of extreme weather events such as freeze-thaw cycles, rain-on-snow and winter warming have already been observed in many areas of the Arctic and the subarctic region (Vikhamar-Schuler et al. 2016).

Predictions of climate change in the Arctic have a high uncertainty, due to the complexity of feedback processes influencing the climate system in this region, such as sea ice melting and associated albedo changes. In the Canadian and Alaskan Arctic, winter temperatures have already risen by 3-4 °C in the past century (ACIA 2005), while winter precipitation in the Arctic is expected to increase by up to 50 % (Räisänen 2008; IPCC 2013), so it is not clear how snow depth and snowmelt timing will change in the future.

Decomposition rates will be higher in warmer soils which then release more CO_2 into the atmosphere, but increases in vegetation cover will also increase the uptake of CO_2 from the air. The balance of these two processes will determine whether northern ecosystems, where about one third of the world's carbon is stored (Gorham 1991), will be a source or sink of CO_2 in the future. In order to answer this question, we need to understand how plants will respond to the projected changes. Some consequences of these changes in climate for terrestrial ecosystems can be shifts in vegetation community composition, most notably the expansion of shrubs, and alterations in biogechemical cycles, especially

the carbon cycle (Sturm et al. 2001; Walker et al. 2006; Sakaguchi et al. 2016). However, the magnitude and direction of these changes is not known.

In cold ecosystems, frost exposure and the persistence of snow are important determinants of plant species distribution to the extent that changes in snow cover can lead to changes in community composition (Inouye 2000; Körner 2003; Niittynen and Luoto 2017). Consequently, in order to predict the future persistence of different plant species in a changing climate, we must understand how these species cope with climate variation and how resilient they are with respect to this climate variation.

1.3 EXPERIMENTAL MANIPULATION OF SNOW

Studies on how climate change affects plants have included experimental manipulations of environmental factors, multi-annual historical observations of climate and plant traits and observations along natural environmental gradients (Dunne et al. 2004). Each of these methods bears advantages and limitations regarding the interpretation of the measured plant responses (Dunne et al. 2004; Rustad 2008).

Experiments which simulate changes in snow depth and snowmelt timing have been used widely to study the effect of changing snow conditions on plant life (Wipf and Rixen 2010; Cooper 2014). In these experiments, artificial removal (by shovelling) or accumulation (using snow fences) of snow is used to simulate decreases or increases of snow. These experiments can target the most important environmental factors affecting plants through a controlled and mechanistic approach. However, in experiments only a few environmental factors are manipulated at a time, which does not correspond to the complexity of the whole ecosystem, and other related climate conditions are often not measured to the same detailed level. Some experimental setups also create unwanted artefacts by altering other environmental factors, such as the influence of passive greenhouses on light availability, wind speed and snow depth (Kennedy 1995). It has been shown that these drawbacks can lead to an over- or underprediction of plant responses to climate change (Wolkovich et al. 2012; Blume-Werry et al. 2016).

Short-term experiments capture the short- and mid-term plasticity of plant responses, which give meaningful insight into their initial capacity to cope with novel conditions. In a study of *Salix herbacea* from

the Swiss Alps, it was found that this species exhibits strong phenotypic plasticity and low local adaptation to small-scale, natural variations in snowmelt timing (Sedlacek et al. 2015). Due to the slow adaptive evolution, i.e. the evolution of traits which are adapted to the environment, of tundra plants and their limited dispersal ability, this plasticity is an important trait for growth, reproduction and persistence in a changing climate (Jump and Peñuelas 2005).

1.4 MICROCLIMATIC VARIATION OF SNOW

Long-term historical observations of climate and plant traits show how plants have responded to climatic changes in the past (Walker et al. 1994). They comprise changes in species interactions, ecosystem dynamics and feedback mechanisms and therefore give a complete account of how plants are affected by climate (Dunne et al. 2004). However, the historical rates and magnitude of change may not correspond to future climates so the past responses cannot be translated directly into future predictions.

While experimental manipulations of the environment reveal the plant's short-term phenotypic plasticity and its capacity for initial resilience, they do not give information about the long-term evolutionary adaptation of plant populations to natural variations in their habitat. Above the treeline in the tundra, the uneven landscape topography creates distinct microclimates, that is, climatic variation on a small spatial scale of a few metres (Scherrer and Körner 2010). The distribution of snow is especially affected by topography, as wind blows the snow from elevated ridges in the landscape and causes its accumulation in sheltered depressions. Areas with different snow depths and snowmelt timing can be adjacent to or within a few metres of each other, thereby creating divergent microclimates for plant populations (Körner 2003). The snow cover also exerts a strong control on the thermal differentiation of habitats, as early-melting vegetation patches with low snow cover experience more variable and lower winter temperatures as well as more early-spring frost events than late-melting snowbeds. Late-melting snowbeds with deep snow cover, on the other hand, have more stable winter temperatures and experience more moderate spring temperatures upon melt-out later in spring (Kimball et al. 1973). These temperature differences experienced by short stature plants are not reflected in weather station temperatures which are usually measured about 2 m above the ground, and used in climate change modelling (Scherrer and Körner 2010, 2011; Scherrer et al. 2011; Aalto et al. 2017).

Microclimate heterogeneity creates intra-population diversity in plant traits, as plant populations exposed to microclimatic differences must have adapted to the differences in order to persist (Opedal et al. 2015). It has been suggested that populations from relatively heterogeneous habitats also have a greater adaptive capacity than those from homogenous ones, because the greater amount of specialisation of different ecotypes extends the amount of habitats a species can live in (Crawford 2008; Scherrer et al. 2011). Landscape heterogeneity also allows the preservation of diverse habitats. These may serve as suitable niches in close proximity to former habitats and retain a suitable microclimate even as the regional climate changes (Armbruster et al. 2007; Scherrer et al. 2011).

The study of natural climate gradients as a proxy for future climate change is based on the assumption that plants respond to spatial climate variability in the same way as to the temporal variability expected from climate change (Dunne et al. 2004). However, the long-term adaptation of plant species and covarying environmental conditions along gradients limit the use of natural gradients as space-for-time substitutions. A combination of experimental and observational approaches is therefore needed to fully understand how plants respond to climate change.

Climatic variation, whether due to climate change, experimental manipulation or microclimate heterogeneity, requires plants to adapt to this variation in order to persist. Little is still known about how plants respond to natural variations in microclimate and how they are affected by it.

1.5 PLANT PHENOLOGY AND SNOWMELT

Due to the short growing season and harsh winter conditions at high latitudes, the timing of seasonal events (phenophases) in plants, relative to the timing of snowmelt, is crucial to plant performance. Plants which initiate growth rapidly after snowmelt may benefit from a longer growing season and thus increase the time available for carbon acquisition, growth and reproduction. On the other hand, they risk frost damage and oxidative stress on the photosystem due to premature dehardening when temperatures are still low and fluctuating (Cannell 1985; Hänninen 1991; Adams et al. 2002, 2004; Saarinen and Lundell 2010). Differentiating and young tissues are especially sensitive to frost damage and may be killed off completely by frost (Inouye 2000). In the case of reproductive buds, frost damage can reduce the number of flowers in the following

growing season with consequences for seed production, seedling recruitment and population persistence (Inouye 2008). Furthermore, changes in phenological timing may cause mismatches between flowering and the peak presence of pollinators, possibly leading to decreased fitness for insect-pollinated plants (Høye et al. 2013). It is therefore hardly surprising that the timing of bud burst and flowering have been shown to be tightly linked to snowmelt timing in some species (Wipf et al. 2009; Wipf and Rixen 2010; Cooper 2014).

Many studies have focused on only a few key phenological events, such as leaf unfolding and peak flowering, to find out if there are any patterns in the responses of plant phenology to snowmelt timing. Some studies have suggested that this response may be dependent on growth form or temporal niche of a species within the season (e.g. whether a species is generally early-flowering or late-flowering), but a general consensus is lacking (Wipf 2010; Petraglia et al. 2014; Khorsand Rosa et al. 2015; Livensperger et al. 2016).

1.5.1 SPRING PHENOLOGY

In temperate and boreal tree species, winter chilling, winter and spring temperature and photoperiod have been identified as the main factors affecting the timing of budburst (Körner and Basler 2010). However, in these regions, the growing season is longer and snow cover has smaller effects on trees of tall stature compared to low stature plants. The influence of photoperiod on the phenological cycle of tundra plants is not as clear. Keller and Körner (2003) found that only about half of the species from the Austrian Alps which they studied were photoperiodic, i.e. the timing of their flowering responded to photoperiod. Photoperiodism confers the advantage of preventing growth upon unusually early snowmelt, when temperatures are still low. In early-developing species and those growing at higher altitudes, photoperiod can even pose a constraint on the temperature response of the onset of growth (Keller and Körner 2003; Hülber et al. 2010).

In contrast to alpine tundra, Arctic tundra experiences a 24 h photoperiod between May and July, depending on the latitude, so photoperiod is likely a less important cue for Arctic than for alpine spring phenology (Ernakovich et al. 2014). Winter temperatures are lower and snow cover often less consistent in the Arctic compared to the alpine tundra and this delays the thawing of the soil, leading to reduced microbial activity, root activity and nutrient turnover. In the Arctic, low soil temperatures in spring are therefore thought to be instead the

limiting factor controlling spring phenology (Arft et al. 1999; Walker et al. 1999; Smith et al. 2012). The low winter temperatures also imply that any possible chilling requirement, i.e. the amount of low temperatures required before dormancy can be broken, is usually met, leaving snowmelt timing and spring temperatures as the main drivers of bud burst in the Arctic (Pop et al. 2000).

1.5.2 AUTUMN PHENOLOGY

While early phenophases are often controlled by snowmelt timing, it has been shown that the duration of phenological periods (phenoperiods), e.g. the time from bud greening to leaf senescence, is constant in some Arctic plant species regardless of snowmelt timing (Semenchuk et al. 2016). This implies that in these species, the timing of snowmelt can indirectly affect the timing of autumn senescence through its effect on bud greening (Semenchuk et al. 2016). In deciduous species, the timing of leaf senescence is important for ensuring a long growing season and sufficient time for nutrient resorption and the development of dormancy, all of which affect subsequent plant survival and performance. The resorption of nutrients, especially nitrogen, from senescing tissue, greatly increases the resource economy of new growth in the spring and allows rapid growth as soon as the conditions are favourable (Jordan et al. 2012; Estiarte and Peñuelas 2015). Nutrients which are recycled internally can be used to promote new growth quickly without using resources for the acquisition of new nutrients or waiting for favourable soil temperatures which allow nutrient uptake from the soil (Jordan et al. 2012).

The depth of winter snow can also affect autumn senescence through resource acquisition as it alters soil moisture and nutrient availability. The increased soil moisture near late-melting snowbanks has been associated with delayed senescence (Cooper et al. 2011). Deeper snow also retains more nutrients in the snowpack and increases the winter soil temperature which allows increased nitrogen mineralisation by microorganisms and increased leaf nitrogen content (Schimel et al. 2004; Semenchuk et al. 2015). The relationship between leaf or soil nutrient status and timing of leaf senescence in relation to snow depth is currently unclear, but higher leaf nutrient content and later senescence in *Salix polaris* growing under deep snow at the same site as in (III) suggest that deeper snow alters the progression of senescence through delayed nutrient resorption (Abbandonato 2014; Semenchuk et al. 2015).

At the end of the growing season, decreasing temperature and photoperiod provide a cue for the plants that winter is approaching.

Photoperiod has been suggested as a possible driver of autumn phenology in some studies where the timing of senescence did not vary despite differences in snowmelt timing and increased temperature (Barnes et al. 1998; Arft et al. 1999). In contrast, NDVI data from Marchand et al. (2004) shows that autumn senescence is delayed by warming, implying a temperature sensitivity of this process. In contrast, a meta-analysis covering 12 sites between 1992 and 2009 found that autumn senescence advanced with higher temperatures (Oberbauer et al. 2013). Especially in shrub-dominated tundra, autumn senescence has been found to be more responsive to warmer temperatures than spring bud burst (May et al. 2017). The contrasting responses of autumn senescence to climate variation described in the literature highlight that we do not fully understand yet what drives autumn senescence in plant species from the Arctic tundra. Despite this, autumn senescence in tundra plants is still less studied than early phenophases (Gallinat et al. 2015).

1.6 LOW TEMPERATURE-INDUCED PHOTOSYSTEM STRESS

Photosynthesis in the winter is thought to be limited by air temperature, but the mild conditions under the snow have been shown to allow photosynthesis to continue in winter in some evergreen fieldlayer plants, such as *Vaccinium vitis-idaea*, *Ledum palustre* and *Cassiope tetragona* (Lundell et al. 2008, 2010; Saarinen and Lundell 2010, Starr and Oberbauer 2003). During winter, boreal *V. vitis-idaea* overwintering under approximately 20 cm of snow cover had a lower light compensation point in January-April than during the rest of the year, so that the subnivean photosynthesis was sufficient to compensate for wintertime respiration loss of carbon (Lundell et al. 2008).

Photosynthesis of C_3-type plants can be separated into a light-dependent and a temperature-dependent process. In the light-dependent process, the absorption of a photon from solar radiation excites an electron in photosystem II (PSII), which is subsequently passed down the electron transport chain where it creates a proton gradient across the chloroplast membrane. The proton gradient is dissipated via a transmembrane ATPase, creating ATP and NADPH in the process. In the temperature-dependent process, the ATP is used to drive the Calvin cycle, a temperature-dependent cycle of enzyme reactions, which oxidise

NADPH and CO_2 and create a three-carbon sugar molecule used as a precursor for more complex carbohydrates.

The balance between the light-dependent and temperature-dependent processes of photosynthesis is important to prevent an excess of electrons. Excess electrons generated during the light-dependent part of photosynthesis can lead to the formation of reactive oxygen species (ROS) (Foyer et al. 1994). Under normal conditions, the protection against ROS-induced photooxidative damage occurs via thermal dissipation of the absorbed light energy, increased cycling of electrons around photosystem I and inactivation of PSII. Adverse environmental conditions, such as pathogens, UV radiation or low temperature, can slow down the Calvin cycle as well as the protection and repair mechanisms, leading to an increase in ROS production and decreased repair of photooxidative damage. Plants possess several mechanisms to avert this risk during unfavourable winter conditions, such as the thermal dissipation (non-photochemical quenching, NPQ) of the photon energy by the photosystem II protein complex and light-harvesting antennae aided by zeaxanthin (Li et al. 2000). This mechanism can be activated transiently upon exposure to light during unfavourable conditions (e.g. low temperatures) or it develops during winter hardening (sustained NPQ) and is released in spring upon return to favourable weather conditions (Adams et al. 2004). Damage to the photosystem II and NPQ both result in a reduced quantum yield of photosystem II (ΦPSII) (Adams et al. 2002, 2004).

Low temperature limits CO_2 uptake, creating an imbalance between the temperature-insensitive absorption of light energy and the temperature-sensitive Calvin cycle (Öquist and Huner 2003). Additional stresses such as winter drought can further decrease ΦPSII (Neuner 1999). The degree of reduction in ΦPSII caused by a combination of high irradiance and low temperature depends on the temperature sensitivity of plants and the actual temperature and irradiance. Plants with lower temperature sensitivity usually experience a lower reduction in ΦPSII when exposed to high irradiance and low temperature than plants with high temperature sensitivity (Hetherington et al. 1989). Higher irradiance and lower temperatures both increase the reduction in ΦPSII (Germino and Smith 2000). In Scots pine, the quantum yield of photosynthesis is correlated to three-day minimum and maximum temperatures and this corresponds to the changes in ΦPSII seen during frost hardening (Öquist and Huner 2003).

Dwarf shrubs are particularly susceptible to low-temperature light stress, as low or lacking snow cover exposes them to a combination of low

temperatures and high solar irradiance (Neuner et al. 1999; Gerland et al. 2000; Saarinen and Lundell 2010; Taulavuori et al. 2011). Both early snowmelt in spring and patchy snow cover in winter can induce low levels of ΦPSII (Neuner et al. 1999; Lundell et al. 2010). As the snow is melting in spring, dwarf shrubs such as *V. vitis-idaea* are quickly exposed to increasing levels of light and low air temperature. This leads to a rapid decrease in ΦPSII shortly before leaves are fully exposed and for several days after snowmelt (Lundell et al. 2010). Within a few few weeks after snowmelt, *V. vitis-idaea* fully recovers from this reduction in ΦPSII (Lundell et al. 2008). It is not known yet how photoinihibition varies among individuals exposed to differences in snowmelt timing. As photoinihibition is reversible and does not cause sustained damage to the plant, it can give insight into the degree of stress plants can tolerate under present climate conditions.

1.7 FROST DAMAGE

Low temperatures can also cause direct damage to plants either through mechanical damage of the cell membrane or indirectly by impairing protein function. Mechanical damage occurs through the formation of ice which damages the cell membranes. Extracellular freezing water in the apoplast causes cellular dehydration and may lead to the death of the cell. Intracellular ice formation, if not prevented, is lethal to the cell as it can disrupt the internal structure of the cell. The fluidity of cell membranes also decreases when temperatures drop, which impairs their function and makes them more prone to damage. Furthermore, enzyme function is impaired if the temperature is below their optimum temperature threshold.

Plants acclimated to cold environments either need to avoid this frost damage, e.g. by growing only in late-melting snowbeds and developing late, or they must have evolved physiological strategies to cope with freezing temperatures. Mechanisms conveying frost resistance to plants include avoidance of frost damage by supercooling and tolerance of extracellular freezing (Neuner 2014). Supercooling allows the intracellular water to cool down below its freezing point while remaining in a liquid state, but this process has a temperature and time threshold, so it cannot be sustained for longer freezing periods (Schulze et al. 2006). Tolerance of extracellular freezing is accomplished by desaturation of cell membrane lipids, which makes them more fluid and less prone to rupture (Uemura et al. 2006). Furthermore, the accumulation of antifreeze

proteins inside the cell delays intracellular ice nucleation and increasing the amount of osmolytes in the cytoplasm reduces dehydration (Guy et al. 1992). Sklenář (2017) studied mechanisms of frost resistance in temperate-alpine plants, including the common tundra dwarf shrubs *Vaccinium vitis-idaea* and *Dryas octopetala*, and found that they vary in the degree to which they employ supercooling or frost tolerance or both of these mechanisms.

The ability of plants to survive frost, termed frost hardiness, varies with plant species, season and the preceding temperature and moisture conditions, which initiate the development of hardiness (Sklenář 2017). However, snow cover plays an additional role in the degree of hardiness, as a sheltering snow cover can reduce frost resistance (Saarinen and Lundell 2010; Palacio et al. 2015). This was especially apparent under laboratory freezing treatments in *V. vitis-idaea*, which exhibited frost hardiness down to -80 °C from habitats without snow cover compared to -40 °C from habitats where it was protected by snow (Taulavuori et al. 2011). This difference in frost hardiness was also seen in the increase in cell damage measured in *V. vitis-idaea* growing in an exposed versus a sheltered subarctic-alpine site (Saarinen and Lundell 2010). However, it is not known how much frost damage varies among individuals of *V. vitis-idaea* exposed to variations in snowmelt timing on a small spatial scale. Similarly to photoinhibtion, sub-lethal levels of frost damage can be used to estimate the degree of physiological stress a population can cope with. This can give insights into the population's resilience to the predicted increases in the frequency of spring frost events.

2 AIMS OF THE STUDY

In this dissertation, I examined how differences in snowmelt timing and temperature affect subarctic-alpine and arctic plants. The aim of this study is to get a better understanding of the environmental variation plants cope with in their natural habitat, how this variation affects them and whether their responses can be compared to those exhibited in experimental studies.

In Article I, I discuss how natural differences in snowmelt timing affect the timing and rate of phenological development in subarctic-alpine plants. Article II describes how these natural differences in snowmelt timing modify the microclimate in a subarctic-alpine habitat of *Vaccinium vitis-idaea* and whether the differences in microclimate cause any reduction in ΦPSII or increase in cell damage in the plants. I also investigated the parallel use of experimental and natural gradients of snowmelt timing and their effect on the onset of autumn senescence in High Arctic plants (Article III). Lastly, I studied whether autumn warming alone, rather than whole-season warming, affects the timing of senescence in High Arctic plants on Svalbard. (Article III).

3 MATERIALS AND METHODS

The materials and methods used in this dissertation are described in detail in the Articles I, II and III, as indicated in Table 1. Summaries of the study sites and the main methods can be found below.

Method	Publications
Plant response variables	
Phenological observations	I, III
Chlorophyll fluorescence	II
Electrolyte leakage	II
Environmental variables	
Open top chambers	III
Temperature measurements	I, II, III
Natural snowmelt gradient	I, II, III
Experimental snowmelt gradient	III

3.1 STUDY SITES AND STUDY DESIGN

3.1.1 KILPISJÄRVI

The data pertaining to this dissertation was collected in two locations. The first two studies (I, II) were carried out in a subarctic-alpine site on Saana mountain (69°02′37″ N, 20°51′22″ E) which is part of the Scandes mountain range and located in north-western Finland. Polar day, when

the sun does not set, in Kilpisjärvi lasts from May 22nd to July 25th. The fieldsite is located 1.5 km away from the Kilpisjärvi Biological Station, where the annual mean temperature is -1.9 °C and January and July mean temperatures are -12.9 °C and 11.2 °C, respectively (means from 1981-2010; Pirinen et al. 2012). The average annual precipitation is 487 mm and the average peak snow depth reaches 99 cm in March (Pirinen et al. 2012). The treeline on Saana is formed by mountain birch (*Betula pubescens* ssp. *czerepanovii*) and is at approximately 600 m a.sl. above which the vegetation is subarctic-alpine tundra dominated by ericaceous dwarf shrubs such as *Empetrum nigrum* and *Vaccinium* spp., and *Betula nana* and *Salix* spp.

Two study sites were set up at approximately 700-770 m a.s.l, one on the north-eastern ("North") and one on the south-western ("South") slopes of Saana (Figure 1b). At each site, three areas with sequential timing of snowmelt ("Early", "Mid" and "Late") were identified in 2014 and three plots (two in South-Late) were marked in each area in the same year. In 2015, plots were added to each group of snowmelt timing to make up a total of four plots in each group (Figure 1).

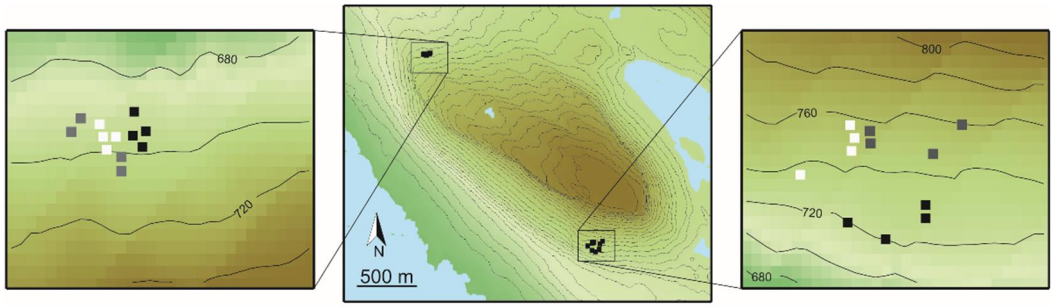

Figure 1 Location of the plots where phenological monitoring was carried out on Saana fell (central image) in 2014 and 2015 (69°02′37″N, 20°51′22″E). The study plots were located on the north-eastern (left image) and south-western (right image) slope of the fell and represent areas with three different timings of snowmelt. Early plots (black squares) melted out between the beginning and the middle of May, Mid plots (grey) melted out between the end of May and the beginning of June and Late plots (white) melted out between the middle of June and the beginning of July. Note that plots are not to scale.

3.1.2 SVALBARD

The Arctic site for study (III) is located in Adventdalen valley (78°11'35"N, 15°55'24"E) on the High Arctic island of Svalbard. Polar day lasts from April 20th to August 20th. At the nearby Longyearbyen airport, the annual mean temperature is -6.7 °C and February and July mean temperatures are -16.2 °C and 5.9 °C, respectively. The mean annual precipitation is 191

mm. The area is underlain by continuous permafrost with an active layer depth of 0.8 to 2.5 m (Humlum et al. 2003). The vegetation on Svalbard is treeless Arctic tundra with dwarf shrubs such as *Cassiope tetragona*, *Salix polaris*, *Dryas octopetala* as well as graminoids. The dominant species varies based on habitat type, as both dry, rocky heaths with shallow soil and taller vegetation and mesic meadows next to river beds with shorter vegetation exist.

In 2006, six snow fences (1.5 m tall and 6.2 m long, distributed over blocks of three fences each) were erected perpendicular to the prevailing winter wind direction (south-east) in each of two vegetation types, mesic meadow ("Meadow") and dry heath ("Heath"). For this study, only one block (i.e. three fences) from each of the two vegetation types were used. The snow fences block the wind and cause an accumulation of snow on the leeward side (Figure 2a). At 2-10 m behind the snow fences, at the site of deepest snow accumulation, three plots (termed "Deep") of 75 x 75 cm were used for this study. Another three plots with medium snow depth (termed "Medium") were marked at 11-26 m behind the fences. Next to the areas of snow accumulation where snow depth was not manipulated, another three plots were chosen as controls (termed "Ambient"). All plots were marked in 2006 for another study (Cooper et al. 2011). Two Deep plots and five Medium plots were substituted for additionally marked plots in 2016, as the originally marked plots from 2006 did not contain all of the species studied here.

Natural snowmelt gradients in Adventdalen valley were determined by observing the landscape topography near the snow fences. In 2016, along elevation gradients in the landscape, three plots were set up on the highest elevated point of a slope where little snow accumulates and snowmelt is expected to occur early (termed "Early"), three plots along the slope with intermediate snow accumulation (termed "Mid") and three plots at the foot of the slope where snow accumulates the most and will melt late (termed "Late") (Figure 2b). The location of Early plots was similar to the Ambient plots so that for two of the gradients in the Heath site, Ambient and Early plots were the same. The terminology for snow groups in the natural and the experimental gradient were distinct due to expected differences between the snow depths.

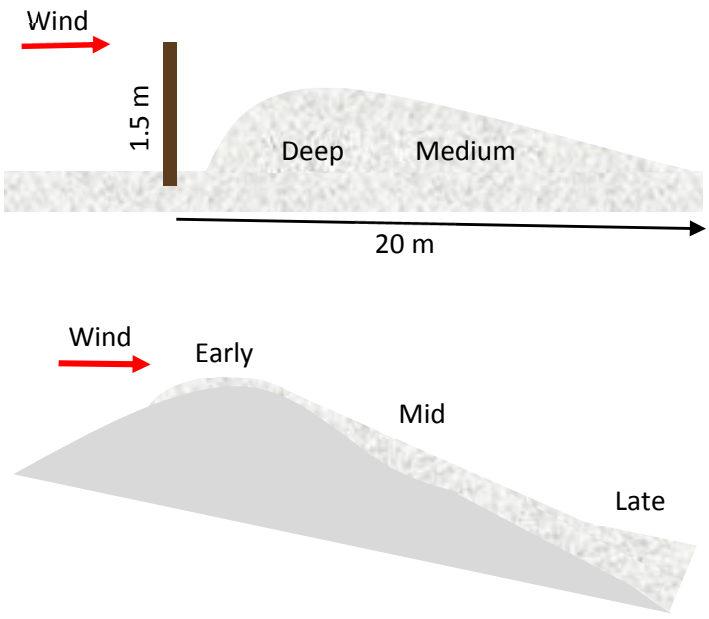

Figure 2 Schematic representation of the snowmelt gradients in Svalbard.

a) Experimental snowmelt gradient created with a snowfence which is positioned perpendicular to the prevailing wind direction. The snow deposits on the leeward side of the fence (brown bar). The highest snow depth (Deep) is closely behind the fence, followed by Medium snow depth. Ambient plots are situated further away from the fence (not shown).

b) Natural snowmelt gradient along a slope. At the top of the slope, wind blows away most of the snow, leaving early-melting snow patches. Along the slope, some snow accumulates creating mid-melting snow patches. Most of the snow deposits at the bottom of the slope where the snow melts late.

3.2 PLANT SPECIES AND PHENOLOGICAL OBSERVATIONS

The plant species used in the phenological observations varied between the subarctic and the arctic site due to differences in the dominant species.

In the subarctic (I), the species were *Betula nana* L., *Empetrum nigrum* spp. *hermaphroditum* (Hagerup) Böcher, *Salix herbacea* L., *Vaccinium myrtillus* L., *Vaccinium uliginosum* L. and *Vaccinium vitis-idaea* L.. In each plot, 24 shoots were loosely tagged with cable ties. The phenophase of all buds on each tagged shoot was observed every three to seven days and the day of year (DOY) on which the first bud on the shoot reached a new phenophases was noted. Observations were made from May 31st to September 2nd 2014 and from May 20th to September 4th 2015.

In the Arctic (III), *Bistorta vivipara* (L.) Gray, *Dryas octopetala* L., *Oxyria digyna* (L.) Hill and *Salix polaris* Wahlenb. were studied. In each plot, only five shoots were tagged with a cable tie or string due to the smaller size of the plots and more sparse vegetation. The shoots were observed every other day from July 19th to August 6th 2016 and the first day of observed autumn colouration on the leaves was noted down.

The following phenophases were measured (in the Arctic, only leaf senescence was measured):

Vegetative phenophases

- Bud green (first evidence of green colour can be seen on the bud)
- Leaf unfolded (the bud has broken open and the first leaf has separated from the bud)
- Leaf expanded (the leaf is fully unfolded and the leaf angle is similar to mature leaves)
- Leaf senescence (first evidence of autumn colouration is visible on the adaxial leaf surface; the colour depends on the species)

Reproductive phenophases

- Flower open (the petals have fully opened; stamens and styles are fully extended)
- Flower senescence (the petals are dry or have fallen off and stamens and styles have withered)
- Fruit set visible (first evidence that the ovary is swollen)
- Fruit ripe (the fruit is completely ripe).

3.3 TEMPERATURE MEASUREMENTS AND TEMPERATURE MANIPULATION

Temperatures were measured at hourly intervals with iButtons® (DS1922L-F5 thermochrons; Homechip Ltd., UK). In Kilpisjärvi (I, II), two loggers were placed at the soil surface, two at 10 cm depth into the soil (rooting zone) and two at 10-15 cm above ground (air temperature) in each plot from spring 2014 to autumn 2016. The air temperature loggers were shielded with a cylindrical white PVC plastic sheet (height = 15 cm, diameter = 6 cm) placed around the loggers. Some loggers broke in subsequent years or were moved to the additional plots set up in 2015, so the number of loggers per plot varied in 2015-2016.

In (II), the temperature measurements were used to calculate the number of days with temperatures below freezing, the number of freezing events (continuous periods with temperatures below freezing) and their duration in hours. The minimum temperature of each freezing event was also extracted.

In Svalbard (III), less loggers were available, so only soil surface and air temperature were measured. Loggers were placed in one or two plots

per snowmelt group in each gradient and site. About 40 % of the loggers broke during the study. Additional temperature data was available from Tinytag temperature loggers (Gemini Data Loggers, UK) placed at the soil surface several years earlier for another study (Cooper et al. 2011).

Five-sided OTCs made of Plexiglas® (Henry and Molau 1997; Marion et al. 1997) were set up on July 20th 2016 to simulate autumn warming and extend the potential growing season directly preceeding the beginning of senescence. Three OTCs were placed near the control plots in each of the three groups of snowmelt timing (Early, Mid, Late) in one of the natural snowmelt gradients in the heath site.

3.4 HIGH SOLAR RADIATION AND LOW TEMPERATURE EVENTS

The frequency of simultaneous high solar radiation and low temperature events was calculated by superimposing photosynthetic photon flux density (PPFD) onto the occurrence of freezing events (II). The STRÅNG model of the Swedish Meteorological and Hydrological Institute was used to model PPFD at a resolution of 2.5 km x 2.5 km. For each freezing event, the highest PPFD ($PPFD_{max}$) measured during that event was extracted. A $PPFD_{max}$>500 μmol m^{-2} s^{-1} during a freezing event was considered to be a potentially stressful high-light exposure according to a previous study (Lundell et al. 2008).

3.5 QUANTUM YIELD OF PHOTOSYSTEM II

In study (II), the quantum yield of photosystem II, which is the ratio of variable (F_v) to maximum fluorescence (F_m), was measured in dark adapted leaves of *V. vitis-idaea* as an indicator of stress to the photosystem (Saarinen et al. 2015). In each plot, 24 shoots of *V. vitis-idaea* were tagged and the top leaf was measured after 20 mins of dark adaptation. The measurements were made with a portable chlorophyll fluorometer (PAM-2100, Walz GmbH, Germany) in 2015 and 2016, once shortly after snowmelt ("Spring") and once at the end of July ("Summer"). The latter was used as a reference value for maximum attainable fluorescence in healthy plants. In South Late, fluorescence was only measured in one plot due to a lack of *V. vitis-idaea* in the other late-melting plots on the South site.

3.6 ELECTROLYTE LEAKAGE

The relative electrolyte leakage was used to assess cell damage in *V. vitis-idaea* (II), which can be a sign of feezing injury due to frost stress. It was measured in 2015 and 2016, once shortly after snowmelt ("Spring") and once at the end of July ("Summer"). The latter was assumed to be a reference value for the level of cell damage when no freezing stress was present. In early-melting plots in 2015 and late-melting plots in 2016 in the South, electrolyte leakage was measured three to four weeks after snowmelt. In late-melting plots, no summer measurements were made in 2015.

For each plot (one plot in South-Late), 72 leaves of *V. vitis-idaea* from the previous year were cut up into six approximately evenly-sized segments and split into 24 samples. The samples were rinsed with distilled water and incubated in 20 ml distilled water for 14 h on a shaker at 100 rpm at room temperature. The conductivity of each sample was measured after the shaking and again after killing the samples by boiling them for 60 minutes and cooling them down to room temperature. Electrolyte leakage was measured as the ratio of conductivity of each sample before and after the boiling and converted to percentage.

4 RESULTS AND DISCUSSION

4.1 MICROCLIMATE VARIATION IN HABITATS OF TUNDRA PLANTS

My study shows that in high latitude tundra, the heterogeneous landscape topography causes a large variation in the microclimate on a scale of a few metres (I, II, III). For studying plant responses to a changing climate, the scale of measurements is of major importance, as it has been shown that climate measurements, for example air temperature from weather stations, do not capture the small-scale heterogeneity of plant habitats (Scherrer and Körner 2010, 2011; Scherrer et al. 2011; Aalto et al. 2017). It has previously been shown that topography has a strong impact on the microclimate (Billings and Bliss 1959; McKay and Gray 1981), but it has rarely been quantified for the scale of plant habitats. Here, I show the small spatial scale and magnitude of natural snow and temperature variation in microhabitats of subarctic-alpine and arctic plants and how the plants are affected by this.

The variation in the deposition of snow creates natural gradients in snowmelt timing, but their magnitude differs between subarctic-alpine and Arctic tundra. In the subarctic-alpine tundra of Kilpisjärvi, melt-out times within a few metres ranged from the end of April to the beginning of July between early-, mid- and late-melting plots, depending on the annual variation in snowfall and temperature. The difference in snowmelt timing between early-melting plots and late-melting plots was up to seven weeks within the same year, which is similar in magnitude to the shift in snowmelt timing predicted under climate change scenarios for this region (Jylhä et al. 2009; AMAP 2017). The plant individuals growing along those gradients therefore already experience climatic differences similar to those expected from climate change, and their responses to the natural variations can give considerable insights into the range of environmental variation the plants can cope with. The adaptation to diverse microhabitats under the present climate is potentiated by the repetitive annual pattern of snowmelt timing and may buffer species against future climate change through pre-adaptation (Crawford 2008; Scherrer et al. 2011; Maclean et al. 2015). That means, the adaptive capacity to adjust to large climatic variations already exists within the populations.

In Svalbard, on the other hand, the natural snowmelt gradients I studied spanned only a few weeks, so the plants there will likely be exposed to novel scenarios of snowmelt timing in the future (Callaghan et al. 2011). Crawford (2008) proposes that plants in highly heterogenous habitats will be more robust against climate change, as those populations are thought to comprise a larger range of ecotypes. This implies that the subarctic-alpine plant populations I studied in Kilpisjärvi will be more resilient to climate change than the populations in the High Arctic valley of Svalbard.

Differences in snowmelt timing and snow depth also influence microclimatic differences in temperature. I demonstrated that the severity and duration of frost exposure at the plant level is greatly modified by the microclimate (II). The risk of frost exposure is a major determinant of cold climate plant distribution which underlines the importance of measuring it on a small spatial scale (Inouye 2000; Körner 2003; Niittynen and Luoto 2017).

In the natural snowmelt gradient in Kilpisjärvi, the long-lasting snow cover in late-melting plots protected plants from the common early-season freezing temperatures in the subarctic, so that they were only exposed to periods below 0 °C on five occasions on average (mean of two years and two sites) throughout the growing season, each occasion lasting up to 9 hours (mean=4 hours) and being at most -2.3 °C cold (II). Plants in early-melting patches were exposed to 31 freezing events throughout the growing season (mean of two years and two sites), lasting between one and 17 hours (mean=6 hours) and with minimum temperatures between -9.5 °C and near 0 °C (II). In combination with early snowmelt, plants in the early-melting plots were therefore exposed to 20 events of high radiation coupled with low temperatures, compared to 12 in mid-melting plots and only five in late-melting plots (II).

The lack of the insulating effect of snow cover was also apparent in the rooting zone, where the temperature was lower thanthe temperature at which soil water freezes (-1 °C) in early-melting plots in the spring (Larcher 1957; Sakai 1968; Tranquillini 1982). This could subject the plants to frost drought, since metabolism can be activated if temperatures are high enough and some light reaches the plants (Larcher and Siegwolf 1985). In late-melting plots higher rooting zone temperatures shortly before melt-out mean that evergreen plants underneath the snow can start photosynthesising early, when temperature and light conditions are favourable. This can substantially alter carbon and nutrient dynamics.

The microclimatic heterogeneity forces plant populations to adapt or acclimatise to it in order to persist. This implies that within populations

growing along such gradients, individual plant responses can be expected to vary according to which set of conditions the plants are exposed to. Subsequently, I show how plant phenology and ecophysiology are affected by changes in snowmelt timing and temperatures along natural and experimental gradients.

4.2 MICROCLIMATE EFFECT ON PLANT PHENOLOGY

4.2.1 EFFECT OF SNOWMELT TIMING

The timing of phenophases in plants has traditionally been measured as the day of year on which the phenophase was observed for the first time. However, phenophases are only discontinuous point measurements as a consequence of continuous physiological processes which result in the visible phenophase (Hänninen 2016). These processes require a certain amount of time, depending on the genotype and current environmental conditions, such as temperature. Therefore, the timing of phenophases is controlled by the rate at which the physiological processes to attain them can proceed.

Previous studies have often only focused on few species or phenophases and more commonly reported DOY as the response variable. This makes it difficult to identify more general patterns in the plant responses. In this study, I analysed the rate of phenological development in response to snowmelt timing, measured as the number of days after snowmelt (DAS) required to attain the phenophases (III). The rate of development reflects the restrictions imposed on the plant physiology by a variable environment, such as changing temperature, and the genotype, and is therefore a more comprehensive measure of the influence of snowmelt timing on plant development. It can therefore give insights into the possible drivers of plant phenology. Generlised patterns can also allow researchers to compare plant responses across different studies.

In Kilpisjärvi (I), the timing of phenophases followed three distinct patterns in response to the timing of snowmelt (Figure 3). In phenophases of *V. vitis-idaea* and late phenophases (leaf expanded, fruit set visible) of *P. caerulea*, the rate of development increased with later snowmelt timing leading to synchronous occurrence of those phenophases along the snowmelt gradient (Figure 3a). The faster rate of development in late-

melting plots therefore fully compensates for the later snowmelt. An increased rate of development after late snowmelt was also observed in early phenophases of *P. caerulea* (leaf unfolded, flower open, flower senescence) and *V. uliginosum*, but this rate was lower and did not compensate for the delay caused by later snowmelt timing (Figure 3b). These phenophases occurred on a later day of year in late-melting plots. In all phenophases of *B. nana* and in the bud green of *V. uliginosum*, the rate of development was the same along the snowmelt gradient so that phenophases in late-melting plots also occurred on a later day of year (Figure 3c). Therefore, in these phenophases, the rate of development did not compensate for the delay caused by later snowmelt timing.

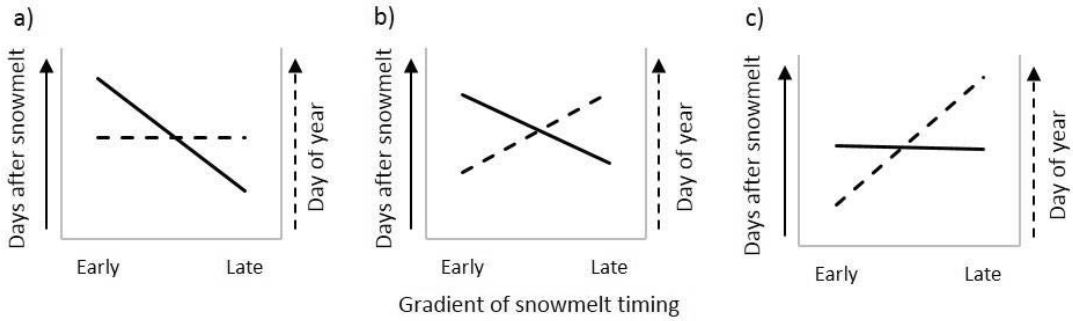

Figure 3 Schematic representation of patterns in plant phenology with regards to snowmelt timing. Phenological timing is represented as days after snowmelt (DAS) until the onset of a phenophase (continuous line) and as the day of year (DOY) of the onset of a phenophase (dashed line). The occurrence of phenophases in response to snowmelt timing clustered in the present study into three patterns: (a) Compensation: The number of DAS required to reach a certain phenophase decreases with later snowmelt timing. This reduction translates into acceleration of growth and compensates for the delay caused by the late snowmelt, leading to synchronous occurrence of the observed phenophases in plots with different snowmelt timing. (b) Under-compensation: The number of DAS required to reach a certain phenophase decreases with later snowmelt timing but this acceleration is not sufficient to compensate for the delayed start of the growing season caused by late snowmelt. Therefore, phenophases are reached at a later DOY in late-melting plots compared to early melting plots, but this difference is smaller than the corresponding difference in the snowmelt timing. (c) Conservativeness (no compensation): The number of DAS required to reach a certain phenophase is the same along the snowmelt gradient. Late snowmelt poses a natural delay to development so that phenophases occur at a later DOY in late- compared to early melting plots and this difference is equal to the corresponding difference in the snowmelt timing.
Note the different slopes in the solid lines in figure parts (a) and (b) and the dashed lines in figure parts (b) and (c).

In the study of High Arctic plants on Svalbard, the timing of senescence in plants was only measured as the day of year and not as the rate of senescence as days after snowmelt. The timing of senescence along the experimental snow depth gradient did not follow one of the linear patterns found in the subarctic region, rather, Medium snow depth caused a delay in senescence compared to Ambient snow depth while

Deep snow depth did not cause any significant shift in senescence compared to Ambient snow depth (III). In the natural gradient, no main effect of snowmelt timing on the timing of senescence was observed (III). These divergent results from experimental and natural snowmelt gradients with similar snowmelt timing underline the importance of considering both experimental and natural gradients when studying plant responses to climate change (Dunne et al. 2004; Elmendorf et al. 2015). Considering only one study approach alone would lead to different conclusions regarding the plant responses. Furthermore, experimental and natural gradients each only address a part of the plants' responses. Experiments, due to their fairly short duration (a few weeks to a few decades), mostly highlight the plants' phenotypic plasticity, while long-term natural gradients give insight into the long-term responses, which may include genetic adaptation.

The timing of phenological events in harsh environments leads to a trade-off between increased plant performance due to a longer growing season and reduced survival due to increased frost damage (Hänninen 1991; Heide 1994; Augspurger 2013). The trade-off might be even more pronounced in the Arctic than the Subarctic, since the growing season in the Arctic is even shorter and the winter conditions more severe. In the Arctic, medium snow depth could be the optimum for plant survival and performance, as it prevents early season frost exposure while allowing a longer growing season than deep snow.

Plant populations growing along snowmelt gradients will experience a completely novel timing of snowmelt in the early-melting plots where climate change will cause even earlier snowmelt than is currently the case. From this study, we cannot predict how plants in early-melting plots will respond to this, but previous studies have used snow removal experiments and transplantations to investigate this (see references in Cooper 2014 and Wipf and Rixen 2010). Where the effect of artificially advanced snowmelt or shallower snow depth on plant performance was measured, the effect was either neutral (Starr et al. 2000) or negative (Wipf et al. 2009), leading to less growth and increased frost damage. In the site in Svalbard of the present study specifically, artificial removal of snow did not increase propagule germination compared to propagules from Ambient plots (Semenchuk et al. 2016).

Contrary to previously published studies, I did not find a correlation between temporal niche of a phenophases or the growth form of a plant and the phenological response to snowmelt timing. The temporal niche of a phenophase or a species, i.e. whether it develops early or late in the season, suggests whether frost (for early phenophases/species) or a short

growing season (for late phenophases/species) impose a greater selective force on the plant. However, early or late phenological timing is not the only way by which frost or a shortened growing season can be avoided, so the temporal niche is not a conclusive predictor of how phenology is affected by snowmelt timing. The temporal niche can also vary within growth forms, for example, evergreen *V. vitis-idaea* is a late-developing species while the evergreen *E. nigrum* develops soon after snowmelt. A recent meta-analysis suggests a strong influence of mean June temperature on the phenology of Arctic plants (Prevéy et al. 2017), but the effects of air temperature are also highly cumulative and strongly correlated with snowmelt timing in cold ecosystems (Semenchuk et al. 2013; Bjorkman et al. 2015). One of the potential drivers affecting the rate of development is suggested to be the accumulation of daily average temperatures above a certain threshold value, termed growing degree days (GDD). Such confounding factors complicate the detection of patterns in the plant responses which can be generalised over growth forms, functional types or taxa.

4.2.2 EFFECT OF AUTUMN WARMING

The extension of the potential growing season by warming with OTCs delayed the timing of senescence only in *D. octopetala*, while senescence in *S. polaris, B. vivipara* and *Oxyria digyna* was not affected (III). Other studies have found a stronger delaying effect of warming on the timing of senescence in several study species (Abbandonato 2014) or vegetation in general (Marchand et al. 2004). In these studies, all individuals of a species within a plot or the canopy as a whole were studied for the progress of senescence while in the present study, only five individuals per plot were measured. Most notably, previous studies have applied warming treatments throughout the whole growing season rather than just part of it. Here, I have shown that a selective warming at the end of the growing season already has an effect on senescence timing. These differences in the methods could be the cause for the incoherence of the results. Senescence as a process lasting from the first colouration of the leaf to leaf fall is slow. Different studies use different stages of the whole senescence process to define it, such as 1 % versus 50 % leaf colouration. This makes it difficult to compare results as they essentially measure different parts of the senescence process. A common measure of senescence timing needs to be defined in the future to be able to draw conclusions from combining study results (Gallinat et al. 2015).

Although the delay in senescence of *D. octopetala* was only approximately four days in the autumn warming treatment, this constitutes a 10 % extension of the 5.5 week-long growing season for this species (Cooper et al. 2011). This is a substantial shift in phenology, also considering that only the end of the growing season was warmed and only the beginning of senescence was observed. A longer period of elevated temperatures could shift the phenology even more and this shift could be amplified in later stages of senescence.

The timing of senescence has a large impact on the whole ecosystem, as ecosystem carbon exchange is correlated with the growing season length (Churkina et al. 2005). Piao et al. (2008) found that higher temperatures in spring increase carbon uptake (photosynthesis) more than respiration in northern ecosystems, while the opposite is true for higher autumn temperatures. The same response of net ecosystem carbon exchange to temperature was found in an Arctic ecosystem (Euskirchen et al. 2012). Considering the projected increases in autumn temperature, this indicates that northern ecosystems could experience a net loss of carbon dioxide in the future.

4.3 MICROCLIMATE EFFECT ON PLANT STRESS

The presence of plants along microclimatic gradients implies that the plants have adapted to the environmental differences in their habitat in order to survive. However, each part of a gradient presents its own challenges, so it can be expected that the degree to which plant physiology is affected also varies. Here, I found that quantum yield of photosystem II (measured as F_v/F_m) was only 0.4 in *V. vitis-idaea* in the spring compared to 0.75 in the summer in all parts of the snowmelt gradient, indicating a reduction in ΦPSII. The potential yield of PSII in *V. vitis-idaea* only starts decreasing when the snow cover is lower than 20 cm in winter and drops substantially for several weeks after snowmelt (Lundell et al. 2008). This is thought to be the result of increased thermal dissipation of the light energy as a response to the cold temperature and high light plants are exposed to after snowmelt in spring (Solanki et al. 2019). The reduction in ΦPSII was 10 % higher in early- and mid-melting plots compared to late-melting plots. This suggests that the PSII function in *V. vitis-idaea* is acclimatised to the variation in snowmelt timing in this habitat.

ΦPSII only declines when stress causes an imbalance between the light energy absorbed and the consumption of energy in metabolic processes (photostasis, Öquist and Huner 2003). In this study, the

frequent spring freezing events are likely the cause of the stress. In a meta-analysis, (Míguez et al. 2015) found a temperature-dependency of ΦPSII declineduring cold periods, where a mean winter temperature of below 0 °C was associated with wintertime increase in NPQ above 50 % in non-tropical plants and a mean winter temperature of above 0 °C was associated with less than 50 % reduction of ΦPSII. A similar kind of temperature-dependency of ΦPSII was found in the present study, since freezing events were common in the spring in early- and mid-melting plots, but there were little or none in late-melting plots.

Contrary to the expectation, cell damage in *V. vitis-idaea* did not correlate with the more severe freezing events seen with earlier snowmelt. The electrolyte leakage was 20-30 % with no clear trends betweens years, sites or along the snowmelt gradient. Similar values were found by, for example, Saarinen and Lundell (2010) and Preece and Phoenix (2013) for *V. vitis-idaea* in the Subarctic. This suggests that there is a considerable amount of cell damage in *V. vitis-idaea* in its natural habitats, but this does not impede its survival. While future projections of increasing freezing events and greater exposure to frost damage due to earlier snowmelt warn about a potential adverse effect on plants, this study shows that substantial levels of stress are well tolerated by one of the very common circumpolar tundra and boreal plant species. However, the responses to climate change, especially extreme events such as winter warming, varies with species and can lead to reduced flower abundance, lower reproductive success, reduced growth and delayed bud burst (Bokhorst et al. 2011, 2017; Semenchuk et al. 2013). Even sub-lethal stress responses, such as increased anthocyanin production, can cause a community-wide decline in productivity, termed “Arctic browning”, which can result in a decrease of net ecosystem exchange (Treharne et al. 2019).

4.4 CONCLUSIONS AND FUTURE PERSPECTIVES

The Arctic and Subarctic are both some of the most fragile ecosystems on Earth and the ones which will be most severely affected by climate change. Due to global feedback mechanisms, the effects of changes in the Arctic will influence the climate system of the whole planet. Researchers are trying to predict how these ecosystems will respond to climate change in order to estimate the consequences for life on Earth. Plants constitute one of the key nodes in ecosystems and are responsible for part of many crucial ecosystem services such as carbon and nutrient cycling, food

production and oxygen and water cycling. It is therefore imparative to understand whether and how they will persist in a changing climate. In order to improve our ability to predict plant persistance, we need to find out their capacity to cope with a changing climate.

The main focus of this study was to understand how plants respond to and cope with natural differences in snowmelt timing which can give insight into the resilience of populations to environmental variation. Evaluating the response of phenology to the timing of snowmelt in terms of the rate of development in addition to the timing of phenophases revealed distinct patterns of adaptation. Plants either compensated for the time lost due to later snowmelt by an increased rate of development or they attained specific phenophases on the same day of year. These patterns can be applied to other species in snow-covered ecosystems and therefore serve as a framework for studying phenology. Furthermore, they can be used to classify past findings of phenological responses. This will allow a common classification of phenological responses to snowmelt timing.

Any patterns we see in the responses of plants to their environment are underlain by physiological mechanisms (Hänninen 2016). We have to understand those mechanisms and their drivers in order to reliably predict plant responses to climate change. The results here show that autumn senescence is especially sensitive to temperature, but the full relationship between environmental variables and the timing, rate and physiology of senescence remains poorly understood. Future research needs to address the gaps between the observed and measured plant responses, the physiological mechanisms behind them and the environmental drivers causing them.

A lot of attention has been brought to the possibility that the expected dramatic changes in climate will lead to the loss of plants and their habitats. While the number of plant species assessed as threatened is rising (IUCN 2018), the results presented here suggest that the threat is not imminent everywhere. The small-scale measurements of climate in this study show that natural plant habitats can be highly heterogeneous, to the same extent or greater than the expected changes in climate. Some of these microclimatic gradients, such as snowmelt timing, are highly conservative from year to year, so that plants have been able to adapt to them through evolution.

Nonetheless, the small spatial scale of these variations means that different, potentially more suitable habitats, are nearby and do not require dispersal over long distances even as the regional climate changes. This study also showed that plants can tolerate a substantial amount of

low temperature stress without lethal damage, so some species may not be as threatened in their existence as assumed. Climate change is not the only future threat to plant populations so the importance of habitat heterogeneity is not limited to retaining climate diversity on a small spatial scale. Perhaps even more than climate, plants are threatened by land-use change, diseases and invasive species (CAFF (Conservation of Arctic Flora and Fauna) 2013), all of which are exacerbated by a lack of diversity on the level of habitats, species and ecotypes. This calls for a wide assessment of current habitats to establish how diverse they are, where they can be found and how we can protect them for the future.

This study alone can barely scratch the surface of the research needed to understand how northern plants will be affected by climate change. Only concerted efforts from large-scale world-wide collaborations can accomplish this task by combining multiple study sites, standardised experiments and long time scales. As researchers, we must remember to work together to understand the world in which we live, and even more so, work with the people inhabiting it.

ACKNOWLEDGEMENTS

This thesis was developed based on my fondness of Kilpisjärvi, which my supervisor Timo Saarinen and our former group member Robin Lundell first introduced me to. This beautiful place was defining for my entire PhD and perhaps for my life, so I am grateful that you showed it to me. It would not have been possible to develop and complete this study without my supervisors Heikki Hänninen and Timo, who entrusted me with the independence to develop my own study in Kilpisjärvi and never once doubted that I could do it. Thank you for all the discussions about ecology and concepts, whether it be in Viikki or through long-distance calls when we were all three in separate countries! Thank you also to Helena for leading our small but sustainable Plant Ecophysiology and Climate Change group throughout the years. You kept our group together and gave me a sense of belonging and you participated in many discussions regarding my PhD.

The staff at the Kilpisjärvi Biological Station made the station became my home for three summers in a row and it would not have been homely without them. You were so friendly and welcoming and helped me improve my Finnish so much. I miss Kilpisjärvi and I hope to go back some day.

The fieldwork would not have been possible without all my field assistants throughout the years: Che, Pasi, Johanna, Sannimari, Katja and Iida. You have enriched my fieldwork experience in so many ways. You were great company and provided great challenges, you helped me keep up my motivation and combat loneliness, you taught me leadership and teamwork. At the same time I must thank Camille, my amazing research assistant in Svalbard. I have loved working and adventuring with you and I hope we will see again one day.

I would like to mention Elisabeth Cooper and Ellen Dorrepaal for their mentorship throughout the years and for sharing their part of the tundra with me. Elisabeth, you have given me the opportunity to immerse myself into Arctic life and research, which is so close to my heart, and I have found kinship in your own stories about your early career development. Ellen, I am glad that we were able to keep in touch throughout the years and that working with you was never cancelled, but only postponed. Thank you for probing me with your questions and seeing in me who I want to become.

I am grateful to the community of the International Tundra Experiment who are so welcoming to newcomers and collaboration and with whom I can share my passion for cold environments. I have found my place among you.

Special thanks to Pedro for his scientific help with R programming, statistics and proof reading, but above all for always being available to talk to. Thank you also to Matt, for answering all my questions about ecology and statistics, for many scientific discussions and for your immeasurable companionship throughout the years. You inspired me to become a scientist and an ecologist. I would also like to thank all the colleagues and friends at the

division of Plant Biology (both former and present), of whom there are too many to mention individually, many of whom I have known since my Master's degree, who have made work and life in the Biocentre so much nicer.

The love of dogs has connected me to special people outside of work and I want to mention their furry companions who brought me friendship: Loki, Nala, Archie, Nina, Wuffy, Frieda, Muska and Nala.

Some friends are really rather family by choice and these people accompanied me in person and in spirit throughout the years: Jeri with Michael and Julie, George, Stephany and Yongmei. You are my soul connections.

Marius, we have been sharing our love for the Arctic and with this inspiration and your support I have made here to complete this work. You have made it survivable and much more than that.

I would not have been able to complete this thesis without the faith my family had in me. Ihr wart immer für mich da und habt für meine Arbeit immer Verständnis gehabt, auch wenn ihr so weit davon entfernt wart. Susi, my furbaby, although you will never read this, I have to tell the world how much I love you and that I will always look after you, as I tell you every single night. We have taught each other unconditional commitment which has taken me through my PhD and will carry me beyond.

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